

# A chronosequence analysis of forest recovery on abandoned agricultural fields in Nicaragua

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**Abstract:** Species composition, diversity and population structure of woody species recovered on three abandoned agricultural fields after 4, 9 and 14 years were characterized. Seedlings, saplings/poles and mature trees were identified and counted in 70 plots of 100 m<sup>2</sup> in each abandoned site. A total of 13, 29 and 22 families represented by 17, 48 and 44 species were registered in 4-, 9- and 14-year-old stands, respectively. There was a shift in dominant species across successional stages. *Lonchocarpus acuminatus* had the highest importance value in the 4-year old stand, whereas, *Myrosporum frutescens*, *Guazuma ulmifolia* and *Cordia alliodora* had the highest importance value in the 9-year-old stand and *Caesaria corymbosa*, *Muntingia calabura*, *Gliricidia sepium* and *Tabebuia rosea* in the 14-year-old stand. The total stem density increased from 5011 to 9631 individuals per hectare as the age of abandonment increased from 4 to 14 years. The total basal area of individuals  $\geq 1$  cm d.b.h. also increased with the age of abandonment. Overall, small individuals ( $< 10$  cm dbh) contributed to more than half of the total basal area. Species diversity was the highest in the 9-year old stand followed by 14- and 4-year-old stands. We concluded that floristic composition of secondary forests recovers rapidly to the mature forest level compared to structural attributes, which is consistent with the general successional trajectories of tropical dry forest.

**Keywords:** Central America; dry forest; Neotropics; restoration; secondary succession; abandoned agricultural field; forest recovery

## Introduction

Tropical dry forests are one of the most degraded and threatened forest ecosystems in Central America (Janzen 2002). Historically, this forest formation has been extensively converted into other land use types, such as agricultural fields and/or range lands (Janzen 2002). The forest remnants probably represent less than 2% of the original dry forest along the Pacific coast of Mesoamerica, an area extending from Panama to western Mexico (Sabogal and Valerio 1998). Dry forests in many areas of Central America are no more pristine old-growth forests, but rather a mosaic of secondary forest formations (Kalacska et al. 2004). In the past few decades, vast forest areas that had been converted to agricultural fields have been abandoned due to shift in the eco-

nomic interest, industrialization and urbanization processes (Thomlinson et al. 1996). Evidence indicates that abandoned agricultural fields have been rapidly recolonized by plants through secondary succession, depending on the severity of land use intensity prior to abandonment (Guariguata and Ostertag 2001). Thus, the study of colonization and vegetation dynamics after abandonment of agriculture plays an important role in shaping our understanding of secondary succession (Peterson and Haines 2000) and enables us to design successful restoration strategies for tropical forest (Aide et al. 2000).

Secondary forests are generally characterized as forests regenerating largely through natural processes after significant human disturbance of the original forest vegetation at a single point in time or over an extended period, and displaying a major difference in forest structure and/or canopy species composition with respect to nearby primary forest on similar sites (Chokkalian and De Jong 2001). Forest succession can be described in four phases (Finegan 1996; Whitmore 1998). The first phase is a dense growth of herbs, shrubs and climbers that rapidly colonize the site and disappear under shade of the emerging small pioneer tree species, which takes place in a short time (1 to 3 years). The second phase is dominated by small pioneer tree species, which emerge and form a continuous woody canopy. They live only for 10–30 years. The third phase is dominated by big light-demanding tree species. Some of these are large pioneers that established simultaneously with the small pioneers in full light, others are strongly light demanding climax species and

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come in during the first three years. This phase takes a long time (75 – 150 years). In phase four climax species establish progressively below phases two and three. Small gaps begin to form as phase 3 trees die, and phase 4 juvenile are released and grow to full height, so that eventually a shifting mosaic steady state forest, reproducing by gap-phase replacement, is re-established. Secondary forests that differ in age generally varies in species composition and this variation has been related to changes in environmental conditions as succession proceeds and to differences among species in terms of their establishment requirements and other life history characteristics (Peña- Claro 2003; Guariguata and Ostertag 2001).

Owing to their socio-economic and ecological importance, their fast-growing properties and the current pressure on remaining old-growth forests, tropical secondary forests have gained much attention and believed to hold enormous potentials for restoration of forest ecosystems (Finegan 1996; Guariguata and Ostertag 2001). Several studies have shown that tropical secondary forests are important sources of timber and non-timber forest products (Chazdon and Coe 1999), and provide environmental services such as protection of soil erosion and sequestration of atmospheric carbon dioxide (Silver et al. 2000). In addition, they are important templates for forest ecosystem restoration and refugia of biodiversity in fragmented landscapes (Lamb et al. 1997). Nonetheless, most of the studies on Neotropical secondary forest succession have been made in wet or humid tropical forests (Brown and Lugo 1990; Finegan 1996; Guariguata et al. 1997; Guariguata and Ostertag 2001; Peñas-Claros 2003). There are, however, few studies that focused on Neotropical secondary dry forest (Janzen 1988; Ewel 1997; Perkulis et al. 1997; Kennard 2002; Kalacska 2004). In addition, many previous studies have been broad investigations without stratification by developmental stages as seedlings, saplings, poles/big trees (Kalacska 2004).

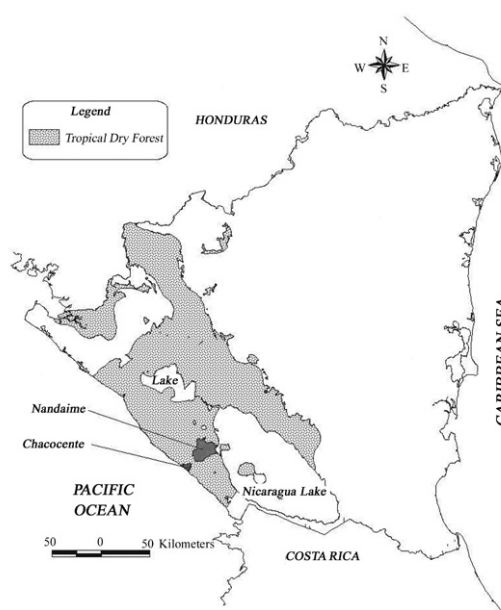
In Nicaragua, studies regarding secondary dry forest succession are very scanty although large forest areas have been converted to agricultural land and recently being abandoned (Chacón and López 1994). Thus, the main objective of this research was to describe species composition, structure and diversity of secondary forests derived from abandoned agricultural fields. We hypothesized that (1) secondary forest attributes vary temporally as succession advances and (2) the presence of remnant trees influence the composition, structure and diversity of secondary forests. The results from the present study are believed to provide base-line information for future management of secondary forests in the country.

## Materials and methods

### Study area

The study was conducted in La Chipopa- Rio Medina community (11° 42' 30" N and 86°05' 30" W), about 7 km south of the city of Nandaime in the province of Granada and 30 km way from Chacocente wildlife reserve in Nicaragua (Fig. 1). The natural vegetation in the area is classified as tropical dry decidu-

ous formation. The dominant dry forest species in the surrounding areas are *Gyrocarpus americanus*, *Tabebuia ochracea*, *Lonchocarpus minimiflorus*, *Caesalpinia exostemma* and *Myrospermum frutescens* (Sabogal and Valerio 1998; Castro-Marín et al. 2005; González-Rivas et al. 2006). The altitude varies from 92 to 167 m.a.s.l. Mean annual rainfall and temperature is 1444 mm and 27°C, respectively. The dry period spans over five months, from December to April. Soils occurring in the area are mainly Vertisols (black soils) and Alfisols (brown soils), originated of volcanic materials and basic rocks from the Tertiary, but soil texture is loamy to loamy franc, with a pH of 7 (Anonymous 1994; Rodríguez et al. 2003).



**Fig. 1** Location of the study area in the vicinity of Nandaime. Close to the study site is the well-known Chacocente Wildlife reserve.

In the 1960s, most forest lands were clear-cut and used for production of agricultural crops (beans, maize, and rice) and for pasture development. In recent years, agricultural and grazing activities have been abandoned. Patches of land were abandoned between 4 and 14 years ago. For the present study, sites were located in three abandoned patches of different ages. The three sites were used for agricultural cultivation and grazing since 1965 but were abandoned and the natural regeneration colonized the sites resulting in young secondary forest. According to key informants (Per. Comm. with Mario Soza and Carlos Soza), the three sites were abandoned 4, 9 and 14 years ago and the size of each site is 1, 3.7, and 4 hectares, respectively.

### Data collection

In each site, 70 plots of 100 m<sup>2</sup> (10 m × 10 m) were established following a systematic design for intensively sampling the secondary forests. In the site abandoned 4 years ago, the 70 plots were allocated continuously along 2 transects. The distance be-

tween two transects was 20 m. In the 9 and 14 years old sites, the 70 plots were allocated along 17 and 8 transects, respectively. The distance between two adjacent plots and transects was 20 m. Each plot was composed of nested quadrats, with smaller quadrats situated within larger one (Sáenz and Finegan 2000) for collecting data by development stages. Thus, within each 10 m × 10 m plot, one 5 m × 5 m subplot was established, and within each 5 m × 5 m plot, one 2 m × 2 m subplot was established in one of the corners. In all 10 m × 10 m plots, we identified and counted all woody species with a diameter at breast height (1.3 m, dbh) ≥ 10 cm. Within each 5 m × 5 m plot, all woody individuals with height above 1.5 m and dbh less than 10 cm were identified and counted. In each 2 m × 2 m plots, all woody individuals from 0.3 m to 1.5 m height were identified and counted by species. For multi-stemmed individual, each stem was considered as an individual. The woody vegetation was classified according to its developmental stage as seedling (individuals with 0.3–1.5 m height), sapling (individuals with 1.5–5 m height and < 5 cm dbh), poles (individuals with 5–10 m height and 5–10 cm dbh), tree (individuals with 10–20 cm dbh) and mature remnant tree (individuals with dbh > 20 cm), following the study by Sáenz and Finegan (2000). Nomenclature follows Stevens et al. (2001), and all scientific names were thoroughly cross-checked in the TROPICOS nomenclatural database of the Missouri Botanical Garden (<http://mobot.mobot.org/W3T/search/Vast.html>).

#### Data analysis

For each site, the total number of species, total number of individuals recorded, and the basal area of all species were computed. The following indexes and parameters were calculated for each site:

1. Shannon - Wiener diversity index ( $H'$ ) (Magurran 2004) using the equation:

$$H' = -\sum P_i \times \ln P_i \quad (1)$$

where  $P_i$  is the abundance of  $i$ th species expressed as a proportion of the total number of stems, and  $H'$  is the Shannon - Wiener diversity index.

2. Structure in terms of: (a) number of individuals per hectare and their distribution in diameter class (for all individuals ≥ 1 cm dbh) and (b) basal area ( $\text{m}^2 \cdot \text{ha}^{-1}$ ) and their distribution in diameter class (individuals with dbh ≥ 1 cm).

3. For all individuals with dbh ≥ 1 cm, the importance value index (IVI) was used to describe the species composition of the plots. IVI of a species is defined as the sum of its relative dominance, its relative density and its relative frequency, which in turn was calculated as follows:

Relative dominance = total basal area for a species/total basal area for all species × 100

Relative density = number of individuals of a species/total number of individuals × 100

Relative frequency = frequency of a species/ sum frequencies of all species × 100

The frequency of a species is defined as the number of plots in which the species is present. The theoretical range for relative dominance, relative density and relative frequency is 0%–100%, thus IVI of species may vary between 0 and 300%.

In order to examine the floristic similarity between sites of different ages, we calculated Jaccard's similarity coefficient,  $C_j$ , using the following equation (Magurran 2004):

$$C_j = j/(a + b - j) \quad (2)$$

where  $j$  is the number of species found in both sites and  $a$  = the number of species in Site A with  $b$  the number of species in Site B. As many of the plots were empty due to the spatially heterogeneous nature of natural regeneration and thus making parametric test difficult due to unbalanced design, Kruskal-Wallis Test and Mann-Whitney U test were performed to compare species diversity, abundance and basal area by developmental stages for stands in a chronosequence.

## Results

### Species composition

We registered a total of 13, 29 and 22 families in 4, 9 and 14 years old stands, respectively. The total number of species in 9- and 14-year-old stands was more than double compared to that of the 4-year-old stand (Table 1). Further analysis of floristic composition by developmental stage indicated that the number of families and species increased with increasing age of abandonment, although the difference was rather small between 9- and 14-year-old stands (Table 2). In the 4-year-old stand, no tree size individual was encountered during the inventory. Four families/subfamilies in the 4- and 14-year-old stands and six families/subfamilies in the 9-year-old stand individually represented more than 5% of the total individuals recorded (Fig. 2). Among these families, Flacourtiaceae and Papilionoideae were present in all sites irrespective of age of abandonment. Families unique to each site were Theophrasteaceae in the 4-year-old stand, Boraginaceae and Sterculiaceae in the 9-year-old stand, and Apocynaceae in the 14-year-old stand. In the seedling class, five species in the 4- and 14-year-old stands and six species in the 9-year old stand individually accounted for more than 5% of the total individuals (Fig. 3). Among these species, *Caesaeria corymbosa* Kunth. and *Lonchocarpus acuminatus* (Schltdl.) M. Souza were found in all sites. While *Jacquinia aurantiaca* Aiton, *Diospyros nicaraguensis* Standl and *Myrospermum frutescens* Jacq were exclusively present in the 4-year-old stand, *Guazuma ulmifolia* Lam. and *Cordia bicolor* A.DC. were unique to the 9-year old stand, and *Lonchocarpus minimiflorus* Donn. Sm. was exclusively found in the 14-year-old stand. Two species, *Acacia costaricensis* Schenck. and *Stemmadenia obovata* (Hook. & Arn.) K. Schum, were found in both 9- and 14-year-old stands.

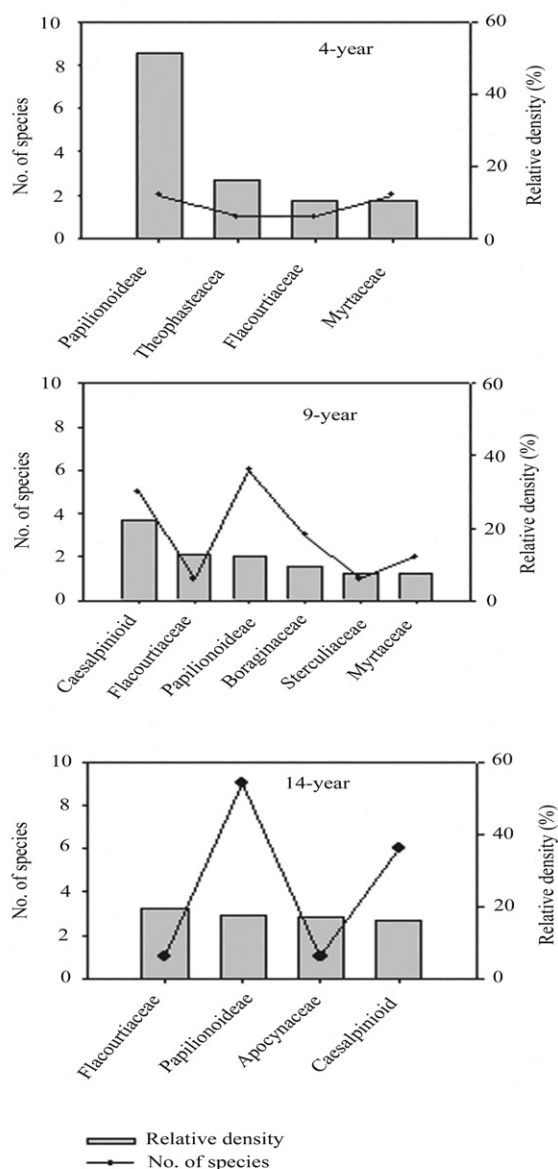


Fig. 2 Families and subfamilies with a percent composition greater than 5% of the total individual in secondary forests recovered after 4, 9 and 14 years on abandoned fields in Nandarola, Nicaragua.

For sapling and pole classes, *L. acuminatus* was the most important species in the 4-year old stand, followed by *M. frutescens* in the sapling class and *Hippocratea rosea* L. in the pole class (Table 3). In the 9-year old stand, *M. frutescens* and *A. costaricensis* were the most important species in the sapling class, *G. ulmifolia* and *L. acuminatus* in the pole class, *G. ulmifolia* and *Caesalpinia exostemma* DC in the tree-size class (Table 3). In the 14-year old stand, the most important species were *C. corymbosa* and *S. obovata* in the sapling class, *Muntingia calabura* L. and *L. acuminatus* in the pole class, *Gliricidia sepium* Kunth ex Steud and *L. acuminatus* in the tree-size class (Table 3). Three species, *M. frutescens* and *C. corymbosa* (in the sapling class) and *L. acuminatus* (in the pole class), were found across all sites. Among the five most important species in the remnant tree class,

it was only *G. ulmifolia*, which was found in the seedling, pole and tree-size classes in the 9-year old stand. In the 14-year old stand, *T. rosea* was found in both remnant tree and sapling classes while *G. sepium* was present in the remnant tree and tree-size classes.

Table 1. Summary of floristic and structural characteristics of dry tropical secondary forests recovered after 4, 9 and 14 years on abandoned fields in Nandarola, Nicaragua.

Stand age	No. of Families	No of Genera	No. of Species	Density (stem·ha <sup>-1</sup> )	basal area* (m <sup>2</sup> ·ha <sup>-1</sup> )
4-year	13	17	17	5011	2.31
9-year	29	44	48	6914	9.17
14-year	22	39	44	9631	10.67

\*(individuals ≥ 1 cm dbh)

Table 2. Floristic and structural characteristics of dry tropical secondary forests recovered after 4, 9 and 14 years on abandoned fields by developmental stage

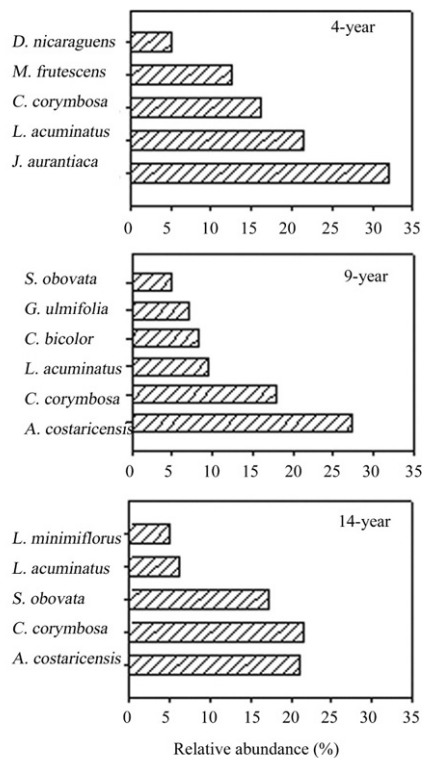
Development stage	Stand Age (year)	No. of family	No. of Species	Stem density (stem·ha <sup>-1</sup> )	Relative abundance	Basal area (m <sup>2</sup> ·ha <sup>-1</sup> )
seedling	4	8	10	2000	39.9	nd*
	9	14	20	3000	43.4	nd
	14	14	22	5786	60	nd
Sapling	4	10	13	2914	58.2	1.49
	9	19	30	3011	43.5	2.89
	14	18	28	2011	20.9	2.09
Pole	4	6	6	97	1.9	0.82
	9	21	29	771	11.2	2.77
	14	19	28	1640	17.0	5.66
Tree	4	0.0	0.0	0.0	0.0	0.0
	9	13	16	103	1.5	1.51
	14	15	21	187	1.9	2.40

\* nd = basal area for seedling class was not computed

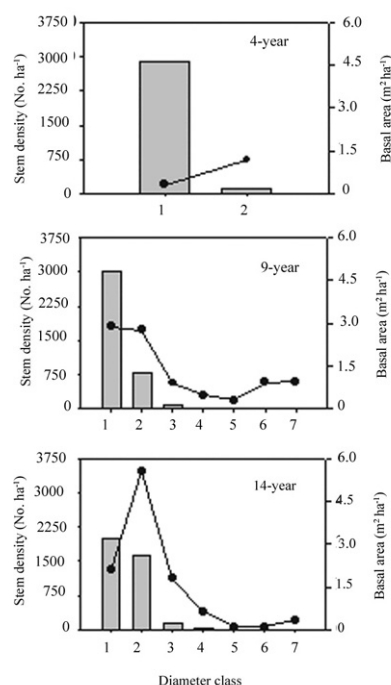
Table 3. The five most abundant species, according to decreasing order of importance value index (IVI in parenthesis), in secondary forest stands by developmental stage

growing stage	4-yr stand	9-yr stand	14-yr stand
Sapling	<i>L. acuminatus</i> (167.8)	<i>M. frutescens</i> (51.0)	<i>C. corymbosa</i> (64.4)
	<i>M. frutescens</i> (56.2)	<i>A. costaricensis</i> (37.5)	<i>S. obovata</i> (48.5)
	<i>C. corymbosa</i> (28.0)	<i>C. corymbosa</i> (27.0)	<i>A. costaricensis</i> (21.6)
	<i>H. rosea</i> (12.6)	<i>D. nicaraguensis</i> (26.2)	<i>M. frutescens</i> (13.0)
	<i>J. aurantiaca</i> (11.0)	<i>L. acuminatus</i> (22.6)	<i>T. rosea</i> (12.3)
Pole	<i>L. acuminatus</i> (179.4)	<i>G. ulmifolia</i> (54.2)	<i>M. calabura</i> (64.1)
	<i>H. rosea</i> (35.2)	<i>L. acuminatus</i> (39.0)	<i>L. acuminatus</i> (41.4)
	<i>A. costaricensis</i> (33.3)	<i>K. calderonii</i> (15.8)	<i>S. obovata</i> (36.6)
	<i>M. frutescens</i> (18.3)	<i>E. salamensis</i> (15.7)	<i>M. frutescens</i> (34.1)
	<i>D. retusa</i> (18.1)	<i>P. macranthocarpa</i> (15.3)	<i>A. costaricensis</i> (21.9)
Tree		<i>G. ulmifolia</i> (94.0)	<i>G. sepium</i> (90.0)
		<i>C. exostemma</i> (60.9)	<i>L. acuminatus</i> (45.5)
		<i>C. bicolor</i> (29.5)	<i>G. ulmifolia</i> (36.0)
		<i>C. vitifolium</i> (26.9)	<i>M. frutescens</i> (23.2)





**Fig. 3** The five most abundant species in the seedling class for secondary forests recovered after 4, 9 and 14 years on abandoned fields in Nandarola, Nicaragua.

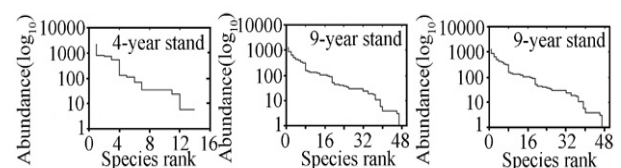


**Fig. 4** Distribution of stem density and basal area of stems  $\geq 1$  cm dbh in relation to diameter class (1 = 1–5, 2 = 5–10, 3 = 10–15, 4 = 15–20, 5 = 20–25, 6 = 25–30, 7 =  $> 30$  cm) for secondary forests recovered after 4, 9 and 14 years on abandoned fields in Nandarola, Nicaragua.

### Stand structure

The total stem density increased from 5011 to 9631 individuals/ha as the age of abandonment increased from 4 to 14 years (Table 1). A similar increasing pattern of stem density was observed for seedlings, poles and tree-size individuals; however, the density of saplings was much higher in 4- and 9-year old stands compared to 14-year-old stand (Table 2). Kruskal-Wallis test revealed significant differences in stem density among stands in a chronosequence for seedlings ( $X^2 = 1.00$ ;  $p = 0.001$ ), saplings ( $X^2 = 7.83$ ;  $p = 0.02$ ) and poles ( $X^2 = 101.50$ ,  $p < 0.0001$ ). The density of tree-size individuals was also marginally significant between 9- and 14-year-old stands (Mann-Whitney U test;  $p = 0.046$ ). For tree-size individuals, stem density in the 14-year-old stand was higher than the 9-year-old stand, and vice versa for remnant trees (Table 2). The total basal area of individuals  $\geq 1$  cm dbh also increased with age of abandonment (Table 1). There was a significant difference in basal area of saplings ( $X^2 = 19.124$ ;  $p < 0.0001$ ) and poles ( $X^2 = 97.059$ ;  $p < 0.0001$ ), while that of tree-size individuals was marginally significant (Mann-Whitney U test;  $p = 0.046$ ) in a chronosequence. The basal area of saplings was higher in the 9-year old stand than 14-year-old stand while the basal area of poles and individuals reached tree-size in the 14-year old stand was twice higher than the 9-year old stand (Table 2).

The frequency distribution of stem density in diameter classes showed a reversed-J shape curve for both 9- and 14-year old stands (Fig. 4), suggesting that individuals with the smallest diameter size were the most abundant. Distribution of basal area in 5 cm-diameter classes also showed that two smallest size classes composed more than 60% of the total basal area of individual  $\geq 1$  cm dbh in the 14 and 9 year-old-stages (Fig. 4). We did not register stems  $\geq 10$  cm in the 4-year old stand, but individuals with the smallest diameter size class was the most abundant and basal area was the highest in 5–9.9 cm diameter class.



**Fig. 5** Species abundance plots for secondary forests derived from abandoned fields after 4, 9 and 14 years in Nandarola, Nicaragua.

### Diversity and similarity

The species-abundance patterns of secondary forests derived from abandoned fields displayed the log series distribution (Fig. 5). The majority of the species in all stands in a chronosequence were represented by few individuals while few species were represented by many individuals. The Shannon-Wiener diversity index, which combines species richness and evenness into a single value, is presented in Table 4 for each stand and developmental stage. Species diversity varied significantly among stands

in the chronosequence for seedlings (Kruskal-Wallis Test  $\chi^2 = 13.201$ ;  $p = 0.001$ ), saplings (Kruskal-Wallis Test  $\chi^2 = 34.291$ ;  $p < 0.0001$ ) and poles (Kruskal-Wallis Test  $\chi^2 = 55.224$ ;  $p < 0.0001$ ). The diversity of tree-size individuals also varied marginally between 9- and 14-year old stands (Mann-Whitney U test;  $p = 0.046$ ). The diversity of seedling was higher in the 9- and 14-year old stands than the 4-year old stand. For saplings and poles, diversity was higher in the 9-year old stand compared to the 14- and 4-year old stands.

**Table 4. Shannon-Wiener's diversity index for secondary forest recovered after 4, 9 and 14 years on abandoned field by developmental stage**

Stand age	Shannon-Wiener's diversity index			
	Seedling	Sapling	Pole	Tree
4-year	1.87	1.26	1.32	0.00
9-year	2.41	2.85	2.87	2.19
14-year	2.40	2.43	2.53	2.30

The similarity in species composition between stands in a chronosequence is shown in Table 5. Pooling all developmental stages together, the similarity in species composition was the highest between 9- and 14-year-old stands. When comparing similarities in species composition between sites for each developmental stage, we found that saplings and poles from 9- and 14-year-old stands had the highest similarity while seedlings from 4- and 14-year-old stands had a considerably higher similarity than the other stands. Species similarity for tree-size individuals was higher between 9- and 14-year-old stands.

**Table 6. Structural attributes, diversity and composition of remnant trees occurring on sites abandoned 4, 9 and 14 years ago. Values in parenthesis are IVI values for each species**

Secondary forest stands	No. of species	Stem density (stem·ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ·ha <sup>-1</sup> )	Shannon-wiener index	Most important species (IVI)
4-yr stand	0.0	0.0	0.0	0.0	
9-yr stand	8	29	2.00	1.87	<i>C. alliodora</i> (96.1), <i>I. spuria</i> (47.6), <i>G. ulmifolia</i> (41.9), <i>C. grandis</i> (36.2), <i>S. humilis</i> (21.9),
14-yr stand	5	7	0.25	1.61	<i>T. rosea</i> (77.9), <i>C. grandis</i> (65.6), <i>G. sepium</i> (56.8), <i>C. speciosa</i> (50.9), <i>C. alliodora</i> (48.8)

## Discussion

A widely recognized forest succession model in mesic environments is based on changing patterns of resource availability and its effect on seedling establishment and growth. According to Peet (1992), four phases of succession are distinguished: Establishment, thinning, transition and steady-state. During the first phase, many seedlings establish under conditions of high light and nutrient availability following forest disturbance. Tree growth enhances competition for canopy space, leading to the death of suppressed individuals and a fairly uniform canopy during the thinning phase. The early cohort of canopy trees die during the transition phase, which in turn increases structural heterogeneity and resource availability (such as light availability) for seedling and understory species. Finally the steady-state

**Table 5. Jaccard's similarity coefficient by developmental stage among stands in a chronosequence in Nandarola, Nicaragua**

Size class	Compared years	Jaccard's Index
Pooled	4 versus 9	22.0
	9 versus 14	57.0
	4 versus 14	24.5
Seedling	4 versus 9	20.0
	9 versus 14	23.5
	4 versus 14	33.3
Sapling	4 versus 9	26.5
	9 versus 14	44.0
	4 versus 14	24.2
Pole	4 versus 9	16.7
	9 versus 14	39.0
	4 versus 14	13.3
Tree	9 versus 14	27.6

### Some characteristics of remnant trees

The presence of remnant trees differed between sites (Table 6), particularly no remnant trees were encountered in the 4-year-old stand during the inventory. In 9-year-old stand, a total of eight species were encountered with *Cordia alliodora* (Ruiz & Pav.) Oken and *Inga spuria* (Willd.) J. being the most important species while five species was found in the 14-year stand with *Tabebuia rosea* (Bertol.) A. DC. and *Cassia grandis* L. f. being the most important. The density and basal area of remnant trees was significantly higher in 9- year than 14-year-old stands (Mann-Whitney U test;  $p = 0.046$ ). The diversity of remnant trees also significantly higher in 9- year than 14-year old stands (Mann-Whitney U test;  $p = 0.046$ ).

phase is reached, which is characterized by formation of gap-mosaic of old growth forests, a combination of gap-formation and gap-filling processes, leading to high structural and spatial heterogeneity. This successional model has described well successional pathways of tropical moist forests (Denslow 2000). Successional pathways of tropical dry forests (TDF) may, however, differ substantially from those of tropical rain forests (TRF), rendering knowledge extrapolations from TRF to TDF inappropriate (Viera and Scariot 2006). Several characteristics affecting secondary succession account for the differences. For example, a greater proportion of tropical dry forests species is anemochoric (Bullock 1995), have low survival rate of seedlings due to water stress while light conditions are not overriding for seedling establishment (Gerhardt 1996), coppicing contributes greatly to regeneration (Vesk and Westoby 2004;

Ky-Dembele et al. 2007), gap formation rates and sizes are low (Dickinson et al. 2001), for most dead trees in mature TDF remain standing.

The results from the present study indicate that the recovery of floristic composition changes with increasing age of abandonment. At the early stage of succession (4 years), three families accounted for 80% of the total individuals recorded. As succession advances, the number of families and species increased. For example, 12 families have represented 87% of the total individuals in the 9-year old stand, and 10 families have accounted for 87% of the total individuals in the 14-year-old stand. There was also a shift in the dominant families in the chronosequence. Fabaceae was dominant in the 4-year-old stand while Fabaceae and Flacourtiaceae were dominant in 9- and 14-year-old stands, respectively. The dominant species by developmental stage also differ across the chronosequence, indicating that species achieve their highest dominance at different time during the succession process. This is in line with the general pattern of floristic and structural recovery following abandonment (Guariguata and Ostertag 2001). During the early stage of colonization, the vegetation is dominated by grasses, forbs and shrubs, which are eventually shaded out by short-lived, light demanding pioneer tree species, such as *H. rosea* and *J. aurantiaca* in the present study. After this period, the canopy is dominated by long-lived, tall-statured, light demanding tree species (e.g. *Diphysa robinoides* and *Gliricidia sepium* in our study), finally the canopy of these secondary stands will be replaced by other shade tolerant species. The low species similarity between 4-year old stand and the other two stands provide further evidence about change in species composition as succession advances.

The recovery of species richness and composition during secondary succession is governed by a variety of factors, such as the intensity of past land use, availability of propagule donors, post-dispersal seed fate as well as abiotic factors (e.g. light, soil chemical and physical properties). It is generally believed that under light-to-moderate land use intensity and when seed sources are nearby, woody plant species richness rapidly increases during secondary forest succession, and takes no more than a few decades after abandonment to reach values comparably to old-growth forest (Guariguata and Ostertag 2001). The presence of isolated remnant trees plays an important role in site colonization by serving as perches and food resources for seed dispersers; thereby facilitating seed dispersal (Holl et al. 2000). In our case, we found 29 remnant individual trees per hectare (> 20 cm dbh) in the 9-year-old stand distributed among 8 species and 7 individuals of five species in the 14-year-old stand but nothing in the 4-year-old stand. Some remnant tree species, such as *G. ulmifolia*, were found abundantly in sapling and poles classes. Apparently, the relatively higher species richness in the 9- and 14-year-old stands could be attributed to better seed dispersal conditions. As a whole, the variation in species composition is related to changes in environmental conditions and to differences among species in term of their establishment requirements and other life history characteristics.

Similarly, structural characteristics (stem density and basal area) and species diversity displayed increasing pattern with age

of abandonment. There was also a marked difference in structure and diversity among developmental stages. The stem density of seedlings consistently increased with increasing age of abandonment. This indicates that the advancement of succession created favorable conditions for seed dispersal and seedling establishment and growth, which otherwise are known to be the major barriers for recovery of secondary forests on abandoned fields (Zimmerman et al. 2000). The stem density and basal area of saplings significantly declined as the age of abandonment increased from 9 to 14 years. This could be related to canopy closure, as the number of individuals occupying the canopy (poles and trees) was higher in the 14-year-old stand than the 9-year-old stand. It is well known that as the canopy closes, the attrition of light-demanding individuals will increase (Finegan 1996; Whitmore 1998). As a whole, these findings are in line with previous studies made in seasonally dry tropical forest in northwestern Costa Rica (Kalacska et al. 2004), abandoned henequen plantation in Mexico (Perkulis et al. 1997), slash-and-burn agriculture in a tropical dry forest in lowland Bolivia (Kennard 2002), secondary succession in Bolivian Amazon (Peña-Claros 2003) and secondary dry forests in Chacocente wildlife reserve in Nicaragua (Chacón and López 1994).

The species-abundance patterns revealed that most of the species in all stands in a chronosequence were represented by few individuals while few species were represented by many individuals; a characteristic typical of many old-growth forests in the tropics (Pitman et al. 1999). Several studies have shown that species diversity increases with age of succession (Perkulis et al. 1997; Kennard 2002; Peña-Claros 2003; Kalacska et al. 2004). In the present study, the 4-year old stand had the lowest diversity for seedlings, saplings and poles compared to the 9- and 14-year old stands. This is because a single species (*L. acuminatus*) had represented 46% of the total number of individuals in the 4-year-old stand while seven species accounted for 50% of the total number of individuals in the 9- and 14-year-old stands. As a whole, the values of Shannon-Wiener diversity index fall within the expected range, which is between 1.5 and 3.5 and only rarely surpasses 5.0 (Magurran 2004).

Mature tropical dry forests have lower species richness, smaller stature, lower basal area, fewer canopy strata, lower leaf area index, and more frequent vegetative reproduction than their tropical rain forest counterpart (Swaine 1992; Holbrook et al. 1995). In line with these differences and other growth traits, succession of tropical dry forests is believed to be floristically simpler, comprises fewer seral stages and more resilient (the speed of return to pre-disturbed mature forest conditions) than rain forests (Ewel 1983; Kennard 2002; Vieira & Scariot 2006), albeit considerable variation in resilience among TDF (Lebrija-Trejos et al. 2008) due to variations in the quality of the reference mature forest – lower quality, faster recovery (Kennard 2002), the land use history of the disturbed sites – higher use intensity, slower recovery (Uhl et al. 1988), the sampling criteria employed, and the extent of isolation of the successional site and the availability of propagules (Wijdeven & Kuzee 2000).

Nonetheless, we attempted to compare the recovery process on abandoned sites with that of slightly disturbed dry deciduous

forest in Chacocente, located 30 km away from our site. According to González-Rivas et al. (2006), the old-growth forest is composed of 29 families and 59 species for trees  $\geq 10$  cm, a category referred as tree-size class in our study. Compared to this finding, the floristic composition recovered rapidly after 14 years of abandonment (cf. 15 families and 21 species for tree-size class). Castro-Marin et al. (2005) have reported 450 individuals/ha with a basal area of 15.62 m<sup>2</sup>/ha for the same old-growth forest. Apparently the recovery of structural characteristics (cf. stem density = 187 ind./ha; basal area = 2.40 m<sup>2</sup>/ha) was relatively slow after 14 years of abandonment. However, this is not surprising given the short time of recovery in the present study. After 40 years of recovery, Martin (2004) found that the basal area of trees was 27% lower in secondary riparian forests than the old-growth forest in the Cordillera Central, Dominican Republic. The slow recovery of structural components can be associated with soil nutrient availability and water stress. The recovery of tree basal area from secondary forests located on nutrient-rich soil appears to proceed faster than on highly weathered, nutrient-poor soils of similar age since abandonment (Tucker et al. 1998). Our finding is consistent with the new forests developed on Puerto Rico's degraded lands, where it is shown that a long time must pass before stand structural attributes approach those of primary forests (Lugo and Helme 2004).

## Conclusion

The chronosequence analysis revealed that floristic composition of secondary forests recovers rapidly to the mature forest level compared to structural attributes, consistent with the general successional patterns of tropical dry forest. The site with large number of remnant trees has correspondingly better secondary forest attributes, suggesting the essential role that remnant trees play in enhancing propagule availability. To accelerate the rate of forest structural recovery, silvicultural measures such as addition of manures (fertilizers), weeding, direct seeding and planting of a mixture of long-lived, light-demanding species should be taken.

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**Appendix 1. List of woody species > 0.3 m height recorded in secondary forests derived from abandoned sites after 4, 9 and 14 years by developmental stage (Sd = seedling), (Sp = Sapling), (Po = Pole), (T = tree) and (RT = Remnant trees).**

Family and subfamily	Species	4 years		9 years				14 years					Life form		
		Sd	Sp	Po	Sd	Sp	Po	T	RT	Sd	Sp	Po		T	RT
Anacardiaceae	<i>Spondia mombi</i> L.					X	X	X		X	X		X		Tree
Annonaceae	<i>Annona muricata</i> L.							X							Tree
Apocynaceae	<i>Stemmadenia obovata</i> (Hook. & Arn.) K. Schum	X			X	X	X			X	X	X	X		Tree
Bignoniaceae	<i>Crescentia alata</i> Kunth	X													Shrub
	<i>Spathodea campanulata</i> P. Beauv.		X												Tree
	<i>Tabebuia ochracea</i> ssp. <i>neochrysantha</i> (A.H. Gentry) A.H					X	X	X			X				Tree
	<i>Tabebuia rosea</i> (Bertol.) A. DC.		X							X	X	X	X	X	Tree
	<i>Tecoma stans</i> (L.) Juss. ex Kunth									X					Tree
Bixaceae	<i>Bixa orellana</i> L.						X								Tree

## Continue Appendix 1

Family and subfamily	Species	4 years			9 years				14 years						Life form	
		Sd	Sp	Po	Sd	Sp	Po	T	RT	Sd	Sp	Po	T	RT		
Bombacaceae	<i>Bombacopsis quinata</i> (Jacq.) Dugand.							X							Tree	
Boraginaceae	<i>Cordia alliodora</i> (Ruiz & Pav.) Oken				X	X	X	X	X					X	X	Tree
	<i>Cordia bicolor</i> A. DC.				X	X	X	X		X	X	X				Tree
Boraginaceae	<i>Cordia dentata</i> Poir.				X									X		Tree
Burseraceae	<i>Bursera simaruba</i> (L.) Sarg.					X	X				X	X	X			Tree
Caesalpinoideae	<i>Bauhinia unguolata</i> L.	X									X	X	X			Tree
	<i>Caesalpinia coriaria</i> (Jacq.) Willd.				X								X			Tree
	<i>Caesalpinia exostemma</i> DC.				X	X	X	X						X		Tree
	<i>Cassia grandis</i> L. f.								X						X	Tree
	<i>Senna atomaria</i> (L.) H.S. Irwin & Barneby, Mem.						X									Tree
Capparidaceae	<i>Capparis odoratissima</i> Jacq.				X											Tree
Chrysobalanaceae	<i>Licania arborea</i> Seem.				X											Tree
Cochlospermanaceae	<i>Cochlospermum vitifolium</i> (Willd.) Spreng					X	X	X					X			Tree
Ebenaceae	<i>Diospyros nicaraguensis</i> Standl	X				X	X			X	X	X				Tree
Elaeocarpaceae	<i>Muntingia calabura</i> L.				X		X	X	X				X			Tree
Euphorbiaceae	<i>Adelia barbinervis</i> Schlecht. & Cham					X	X				X	X				Tree
	<i>Croton reflexifolius</i> Kunth.					X					X					Tree
Flacourtiaceae	<i>Caesarea corymbosa</i> Kunth.	X	X	X	X	X	X			X	X					Tree
Hippocrateaceae	<i>Hippocratea rosea</i> L.	X	X	X		X	X	X		X	X	X				Tree
Meliaceae	<i>Swietenia humilis</i> Zucc.				X				X					X		Tree
Mimosoideae	<i>Acacia costaricensis</i>	X	X	X	X	X	X			X	X	X				Shrub
	<i>Albizia caribea</i> (Urb.) Br & Rose					X					X	X				Tree
	<i>Enterolobium cyclocarpum</i> (Jacq.) Griseb.					X								X		Tree
	<i>Inga spuria</i> (Willd.) J.								X							Tree
	<i>Pithecellobium dulce</i> (Roxb.) Benth.										X	X				Tree
	<i>Pithecellobium saman</i> (Roxb.) Benth.				X				X							Tree
Moraceae	<i>Maclura tinctoria</i> (L.) Steud.						X			X		X	X			Tree
Myrtaceae	<i>Eugenia salamensis</i> var. <i>hiraefolia</i> (Standl.) McVaugh		X			X	X	X								Tree
Nyctaginaceae	<i>Pissonia macranthocarpa</i> (Donn. Sm.) Donn. Sm				X	X	X	X			X	X	X			Tree
Olacaceae	<i>Schoepfia schreberi</i> J.F. Gmel.		X													Tree
Papilionoideae	<i>Ateleia herbert-smithii</i> Pittier.				X					X	X	X				Tree
	<i>Coursetia elliptica</i> M.Souza & Rudd										X	X				Tree
	<i>Dalbergia retusa</i> Hemsl.		X	X		X										Tree
	<i>Diphysa robinoides</i> Benth & Oersted.										X	X	X			Tree
	<i>Gliricidia sepium</i> Kunth ex Steud.					X	X	X		X	X	X	X	X	X	Tree
	<i>Lonchocarpus acuminatus</i> (Schltdl.) M.Souza.	X	X	X	X	X	X	X		X	X	X	X			Tree
	<i>Lonchocarpus minimiflorus</i> Donn. Sm.					X	X			X	X	X				Tree
	<i>Machaerium biovulatum</i> Micheli, Mém									X						Tree
	<i>Myrospermum frutescens</i> Jacq	X	X	X	X	X	X	X		X	X	X	X			Tree
	<i>Piscidia grandifolia</i> (Donn. Sm.) I.M. Johnst					X	X							X		Tree
Rhamnaceae	<i>Karwinskia calderonii</i> Standl., J. Wash..		X				X			X			X			Tree
Rubiaceae	<i>Calycophyllum candidissimum</i> (Vahl) DC													X		Tree
	<i>Chomelia spinosa</i> Jacq.					X	X	X		X	X	X			X	Tree
	<i>Genipa americana</i> L					X	X			X						Tree
	<i>Randia cookii</i> Standl.					X				X	X	X	X			Tree
Rutaceae	<i>Zanthoxylon belizence</i> Lundell.								X							Tree
Sapindaceae	<i>Melicoccus bijugatus</i> Jacq., Enum.				X											Tree
	<i>Thouinidium decandrum</i> (Bonpl.) Radlk.		X			X				X	X	X				Tree
Sterculiaceae	<i>Guazuma ulmifolia</i> Lam.				X	X	X	X	X	X	X	X	X			Tree
Theophrastaceae	<i>Jacquinia aurantiaca</i> Aiton	X	X		X	X				X	X	X				Tree